PAN-PACIFIC ENTOMOLOGIST
62(1), 1986, pp. 24–28

Dominance Hierarchies in *Myrmecophila manni* (Orthoptera: Gryllidae)[1]

GREGG HENDERSON AND ROGER D. AKRE[2]

Department of Entomology, Washington State University, Pullman, Washington 99164-6432.

Myrmecophila manni Schimmer are small, apterous crickets found only in association with ants. Their primary host in southeastern Washington is the western thatching ant, *Formica obscuripes* Forel (Henderson, 1985). A study of these crickets was initiated in 1983 to investigate their biology and relationship with the host ants. Observations of the behavior of the crickets soon revealed that they establish linear dominance hierarchies in the laboratory. Field crickets also establish hierarchies in laboratory populations (Kato and Hyasaka, 1958), but these hierarchies are usually associated with territoriality (Alexander, 1961). The purpose of this paper is to report the hierarchy, how it is established and maintained, and its possible roles.

MATERIALS AND METHODS

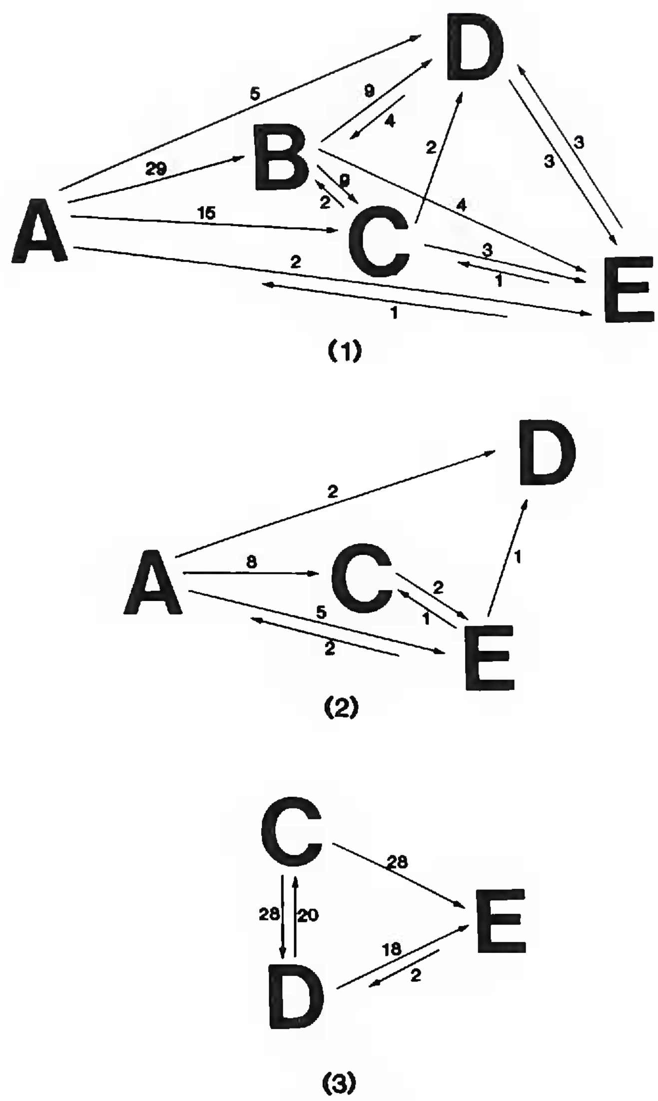
Crickets were collected from colonies of *F. obscuripes* in the vicinity of Pullman, Whitman Co., WA. They were transported to the laboratory in small containers with a layer of plaster of Paris/charcoal in the bottom. This layer was moistened with distilled water to maintain a high humidity since the crickets were very susceptible to desiccation.

Initially, crickets were maintained without ants in 6.5 × 15 cm plastic containers to determine if ants were necessary for their survival (Henderson, 1985). The containers also had a thin layer of plaster of Paris/charcoal that was moistened with distilled water to maintain humidity. Honey on paper toweling was supplied as food, and it was replaced at least once a week.

Observations of aggression between crickets soon developed into the present study on dominance hierarchies. Crickets in three containers were used. One contained 5 adult male and 3 adult female *M. manni.* The males were identified by a letter designation for observations, A–E. Most of the crickets were recognizable by size or general appearance. Males A and B were the largest of the five, and about the same size. However, A was missing one hind leg. Male C was the smallest, with males D and E being slightly larger. The latter were marked with White-out® for rapid identification purposes since they were similar in size. Females were identified, and their behavior was recorded. A second container housed two immature crickets and a single *F. obscuripes* worker. One of these crickets was obviously larger, and was probably a later instar. The third container housed 3 1st instars (1.4 mm), one 2nd instar (1.8 mm), and 2 *F. obscuripes* workers.

[1] Scientific Paper Number 7217, Washington State University, College of Agriculture and Home Economics Research Center, Pullman. Work conducted under project 0037.

[2] Research Assistant and Entomologist, respectively.



Figures 1–3. Diagrammatic representation of dominance hierarchies among male *M. manni.* Letters represent individual males. Numbers indicate the number of aggressive interactions between adversaries. Arrows point from the winner to the loser of the fights.

Most observational periods of the crickets were one hour in duration, and they were made at random times during the 24 hour cycle. A total of 31 recordings were made from 1 July to 22 August 1984.

Results

A linear dominance hierarchy existed among male *M. manni.* Two hundred twenty male–male and 101 female–male aggressive interactions were recorded. Interactions were categorized into four distinct types. Type 1 consisted of a head thrashing duel. Crickets, upon contacting each other, faced off and moved their heads in an up and down swinging motion in an attempt to bring their head over that of their opponent's and to strike downward. This sometimes caused physical damage when the mandibles of one cricket struck the unsclerotized cervical region of the other. Bouts usually lasted about 2 sec and were terminated when one cricket broke off the attack and moved away. Just prior to fully retreating, the loser turned away from the winner, and one or both crickets then shook their cerci in quick, lateral motions of short duration (ca. one sec). Type 2 interactions were characterized by less aggressive behavior than in Type 1. Interactions involved cercal shaking by one or both crickets (as in Type 1 interactions), stilt-walking, (one cricket lifted its body high off the substrate and walked in a slow, stiff gait toward its adversary), or head bobbing, (one cricket moved its head up and down in a manner similar to that in Type 1 interactions but slower and with

Table 1. Frequency of Type 1–4 interactions between crickets.

	Type of interactions				
	1	2	3	4	Total
Male–male interactions	77	109	30	4	220
Male–female interactions	2	14	68	17	101

reduced intensity). Type 3 interactions involved one cricket butting another and chasing the latter from its position. Type 4 interactions were characterized by one cricket lowering its head and body so that it laid flush with the substratum and did not move despite persistent head butts by its opponent, a position, apparently, of complete subordination.

The dominance order in a five male hierarchy, observed from 1 to 20 July is shown in Figure 1. Male A was dominant over the other four crickets, and fought its closest rival, male B, more often than any other opponent ($n = 29$). Similarly, male B fought often with its close rivals, male C ($n = 11$) and male E ($n = 13$). Males D and E did not establish a clear dominant-subordinate relationship since both fought and won equal numbers of fights with each other ($n = 3$ and $n = 3$). In fact, encounters between the more subordinate males were limited. Possibly, their rank in the hierarchy caused them to avoid interactions.

Type 1 interactions were most often observed between close rivals with the exception of male E. Male E interacted with male A in Type 1 displays and was the only cricket other than male B to challenge the dominant male. Interactions between crickets did not appear to become less aggressive over time. Type 1 interactions continued to occur despite the apparent dominance of one cricket over another. However, Type 2 interactions were the most common behavior when crickets came into contact with each other (Table 1).

Upon the death of male B, a new linear dominance was established, but the same dominant-subordinate relationship among the remaining crickets was maintained (Fig. 2). Observations of this hierarchy were made from 20 July to 6 August, at which time male A died. Male E was the only cricket to challenge male A, and on two occasions it inflicted telling blows with its head to the dominant male. Both fights occurred while the crickets were positioned on the wall of the container. Immediately after the mandibles of male E contacted the neck region of male A, the dominant male dropped to the ground and then moved in an uncoordinated fashion as it rubbed its head against the side of the container. This did not, however, seem to give male E an advantage in later battles with male A.

The study was continued 6–22 August with the remaining 3 males (Fig. 3). However, the dominance order of this latter group remained unstable. Males C and D remained dominant over male E, but a single male did not dominate.

Male–female encounters.—Generally, females were much less active than males so that interactions with other crickets were minimal and were usually initiated by males. Interactions between males and females involved mostly Type 3 and 4 interactions. Even the most subordinate male dominated a female. However, just prior to egg laying (ca. three days) a noticeable change in female aggressiveness was evident, and Type 1 and 2 interactions, where females won over males occurred ($n = 15$). In 40, Type 3 interactions males followed females and then went into a mating posture for 1–5 sec (Henderson, 1985). This behavior suggests

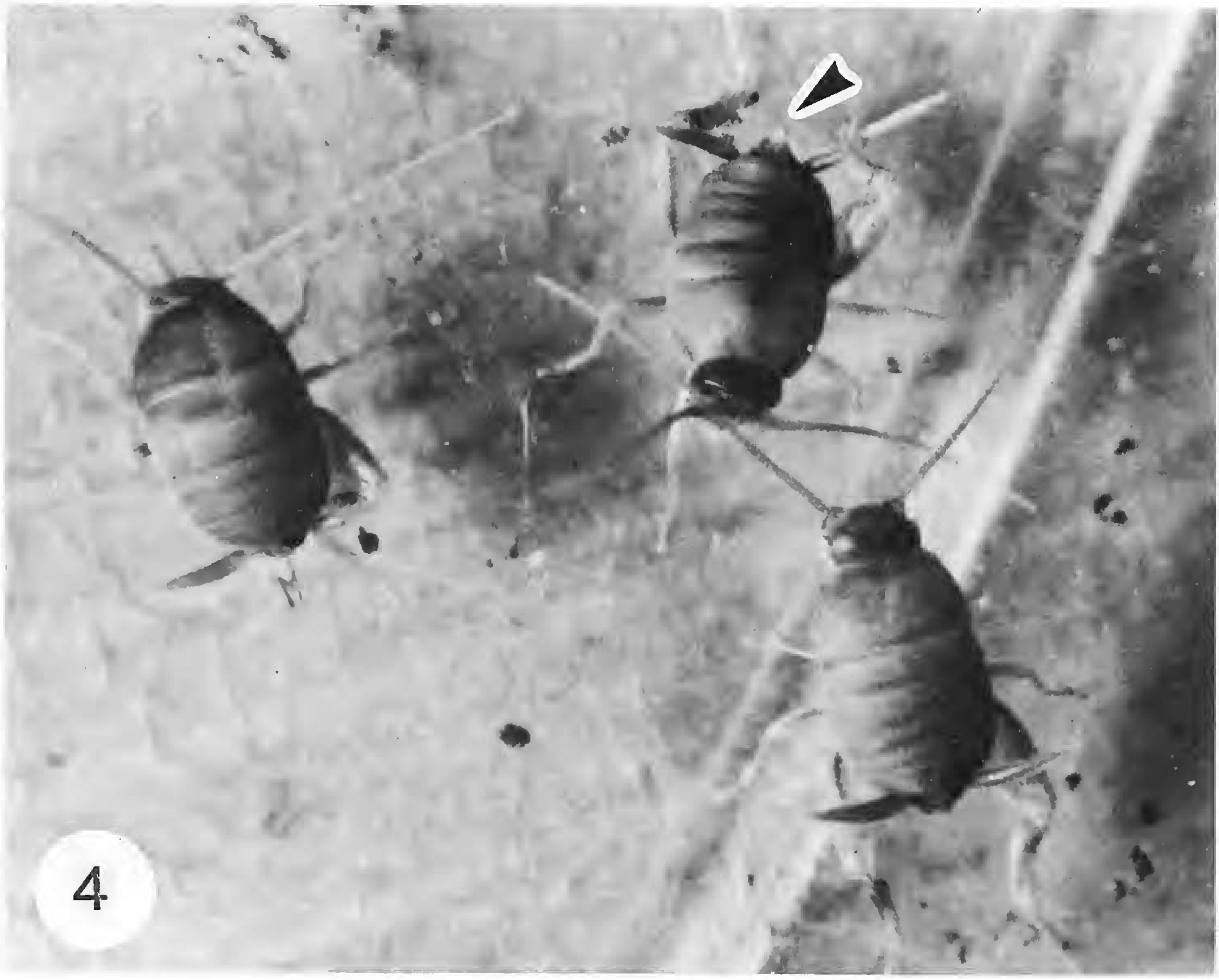


Figure 4. Dominant male interfering in subordinate male's courtship of female. Note spermatophore on the subgenital plate of the subordinate male (arrow).

that males interact with females in an attempt to mate and these interactions probably have little to do with dominance.

Immatures.—Competition among immature crickets was observed as they strigilated and engaged host ants in trophallaxis ($n = 22$). Crickets usually maintained at least a 40° angle, 1–2 mm from other crickets when simultaneously strigilating on an ant. Displacement resulted when crickets were closer than these minimum spacing requirements. Displacement of first instars by second instars indicated that size was a key factor influencing dominance among the immatures. The same dominance relationship was observed in the container with the two larger immatures of undetermined age; the larger dominated the smaller immature. Competition among first instars was also evident but a dominance relationship was not determined because of the difficulty of distinguishing individuals.

Discussion

Size and age seem to play a role in the dominance hierarchies of *M. manni.* Conversely, Alexander (1961) found that age, but not size was a factor in the establishment of dominance hierarchies among field crickets. The large males A and B were always the dominants during this study, and second instars displaced the smaller, first instars to feed on the ants. In addition, the stilt-walking displays in Type 2 interactions also suggest that size is important in maintaining dominance. A similar behavior observed by Holldobler (1976) in competing *Myrmecocystus mimicus* Wheeler ants led him to suggest that stilt-walking is done so that the ant will appear larger and that this had a potential effect on the outcome of the encounter. However, size is obviously not the only factor influencing dominance since male C was much smaller than its subordinates D and E. It is perhaps somewhat ironic that size plays a role in dominance hierarchies in *M. manni* since its myrmecophilous life style, undoubtedly, caused this cricket to be the smallest of all crickets.

All reasons ascribed for the establishment of dominance hierarchies suggest that the dominant individual attains an advantage towards some limiting resource. Nutritional advantages along with an increase in reproduction are associated with dominance in *Polistes* wasps (Pardi, 1948). Nutritional advantages may also be a factor in *M. manni* dominance relationships since immatures fought for trophallaxis or strigulation on a host ant. However, for adult males, mating seems to be the major reason for the establishment of dominance. Successful mating was linked to the establishment of territories in field crickets (Alexander, 1961), but no advantage in fighting by *M. manni* was ever detected due to position in the container. Although males mark areas where they lead females for mating, these areas are not defended and cannot be considered territories (Henderson, 1985). However, subordinate males were sometimes displaced by a dominant when they attempted to mate with a female (Fig. 4) (Henderson, 1985). Although the evidence collected during this study is minimal, it suggests that mating may be one of the primary reasons for dominance hierarchies in *M. manni.*

Acknowledgments

We thank R. Sites, R. Zack, and G. Sehlke for comments on improving the manuscript.

Literature Cited

Alexander, R. D. 1961. Aggressiveness, territoriality and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour, 17:130–223.

Henderson, G. 1985. The biology of *Myrmecophila manni* Schimmer (Orthoptera: Gryllidae). M.S. thesis, Department of Entomology, Washington State University, 83 pp.

Holldobler, B. 1976. Tournaments and slavery in a desert ant. Science, 192:912–914.

Kato, M., and L. Hayasake. 1958. Notes on the dominance order in experimental populations of crickets. Ecol. Rev., 14:311–315.

Pardi, L. 1948. Dominance order in *Polistes* wasps. Physiol. Zool., 21:1–13.